PRESIDENTIAL ADDRESS.

Host and Parasite.

By the late Professor L. Harrison, B.A., B.Sc.

i.—*Introductory.*

I have chosen for the subject of my address the relation between organisms in obligate association under what I call here the host-parasite relation, a matter in which I have been interested for a good many years. The term parasite should, in strict accuracy, be confined to such organisms as live at the expense of their hosts, but I propose to use it loosely to indicate any obligate association, whether parasitic, commensal or symbiotic. Such an association links the parasite to its host in space, as is quite well realized, but curiously little attention has been given to the fact that there is also a linkage in time.

For many groups of parasites host and parasite have come down the ages together. I have dared to fix the origin of bird-lice from psocids as far back as the Jurassic, since there is strong evidence that these existed upon birds and mammals from their very origins, so soon as there were feathers and hair to be eaten. Down that long period of time each generation of hosts has handed on its parasites to its successors. Mammals and birds have changed their forms under the continuous process of evolution, and their lice have changed, too. But parasites in general live under conditions which afford little stimulus to evolutionary change, and so tend to differentiate at a slower rate than their hosts, suffering what I have called elsewhere a retarded evolution.

This relation can be made to serve several useful purposes. The ostriches of Africa and the rheas or nandus of South America are commonly supposed by ornithologists to have arisen from quite distinct stocks. But their lice are so similar, and so different from all other bird-lice, that these must have evolved from a common ancestor, and so also must the birds themselves. Evidence derived from lice is confirmed by the cestode and nematode parasites of the two groups of birds. Thus a phylogenetic relationship may be established by means of parasites. Equally, a supposed relationship may be refuted. Their lice prove that the penguins are in no way related to any northern group of aquatic birds, but belong in an ancient complex which includes the tinamous, fowls and pigeons; that the kiwis of New Zealand are modified rails, and not struthious birds at all; that the tropic-birds are not steganopodes but terns, and so on. A third use is to refute suggestions of convergent resemblance, which are often very lightly made, and which are so exasperating to the zoogeographer since they are usually incapable of either proof or disproof. Leptodactylid frogs are found in South America and Australia. Did they evolve separately, or are they derived from common ancestors? The herpetologist cannot say with any certainty, but the parasitologist discovers that they share a genus, *Zelleriella*, of ciliate protozoan parasites, and must have had common origin. This same example will serve to illustrate a fourth use for the host-parasite relation. The genus *Zelleriella* can, and does, infest frogs other than Leptodactylids. It is not found, however, anywhere except in Australia and South and Central America, so that its distribution affords strong presumptive evidence that South America and Australia have been joined in past time in some way which excluded the northern land masses.

These examples indicate the nature of the host-parasite relation, and its possible usefulness. I propose now to give a short historical account, and to

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follow with an examination of some groups of parasites to see how far this usefulness may be of general application.

ii.—*Historical.*

Since the relation between host and parasite is so obvious, it is remarkable that it has received so little attention. I have searched in vain amongst such textbooks of general parasitology as have come under my notice for any reference to it. It seems incredible that there should not be references in serial literature, but, until quite recent times, I have not been able to trace any. This may be due to the fact that such references, if there be any, occur in papers the titles of which give no indication of this aspect of their contents.

Be that as it may, the earliest use of the host-parasite relation to suggest phyletic affinities which I have been able to trace is that by Zschokke, who in a series of papers (1898, 1899, 1907) upon the cestodes of marsupials, has insisted that the common possession of cestodes of the genus *Linstowia* by South American and Australian marsupials clearly indicated their origin from common stock. Two of Zschokke's papers have not been accessible to me, and I have gathered their content from certain criticisms of Zschokke's views by Nybelin (1917). The latter's criticisms do not seem particularly well founded. They are based chiefly upon the well-known fact that many helminths are viable in animals other than their natural hosts. This must be admitted, but it merely demands that care must be exercised in using the host-parasite relation to distinguish between ancient natural associations and those which if not unnatural, are at least of more recent date. No one would suggest, for instance, because the liver-fluke of sheep has been found both in man and the kangaroo in Australia that these animals had any close genetic affinity with sheep.

Kellogg may perhaps be held to antedate Zschokke, since, in his studies of lice, he drew attention to the fact that parasitic species have persisted unchanged from the common ancestor of two or more distinct but closely allied bird-species as early as 1896. But he was long in committing himself to the conclusion that any use could be made of this relationship, as the following quotations from his writings show. After pointing out that he has taken from American birds a number of lice specifically identical with those described from their European congeners, he writes (1896, p. 51) :—

"This explanation, I believe, is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely allied bird-species. With the spreading of the ancestral bird-species, geographical races have arisen within the limits of the species which have, with time and isolation caused by newly appearing geographical barriers (due to geologic or climatic changes), come to be distinct species—species often distinguished only by superficial differences in colour, etc. The parasites have remained practically unaffected by the conditions which have produced the differences among the birds; the temperature of the host's body, the feathers *as food*, all of the environment is essentially unchanged in its relation to the parasite. The parasitic species thus remains unchanged, while the first *Larus* species or *Anas* species becomes differentiated into a dozen or score of specific forms, all with a common parasite."

Between 1896 and 1913 I can find but one sentence in Kellogg's writings which gives any indication that he was pondering upon the further implications involved in the above statement, and that is (Kellogg and Kuwana, 1902, p. 458) :—

"It was hoped that the character of the parasites found on the strictly Galapagos Island bird hosts might throw some light on the relationships of these birds to continental genera and species . . ."

This hope was defeated by the extraordinary conditions obtaining on the islands, birds of different orders huddling together promiscuously on the bare rocks, and their parasites becoming hopelessly mixed. In 1913, however, Kellogg came definitely, if timidly into the open (1913, p. 138) :—"Of the other Mallophagan genera found on the tinamous two that specially characterize the pheasants and other gallinaceous birds are, by odds, the most commonly represented. And this condition suggests another interesting problem. Is it going to be possible to get suggestions regarding the phyletic affinities of hosts from the character of their parasitic fauna? Take, for example, an order of birds troublesome to the ornithological taxonomists. Will the evidence of the presence on members of this order of certain parasitic genera characteristic of another order indicate their affinities to this second order? It does indeed seem, in the case of the Tinamiformes and Galliformes, as if the evidence from the Mallophagan distribution was in conformity with that suggested by certain structural similarities in the two groups."

In 1914 Kellogg was more emphatic, and he writes (p. 259) :—"Also, if it be true that genetic relationship is the determining factor in accounting for the host distribution of the parasites, then it is also true that the distribution of the parasites will indicate in some measure the genetic relationships of the hosts, and that occasional aid in determining the genetic affinities of birds and mammals of doubtful relationships may be had from a study of their parasitic fauna. In my paper already referred to I have pointed out some suggestive cases of this sort in connection with the birds and their parasites."

He concludes (p. 279) :—"In the light of the plain statement in Part i of this paper of my belief gained from a study of the distribution of the bird-infesting Mallophaga, to the effect that the host distribution of the permanent wingless ectoparasites of birds is determined more by the genetic relationships of these hosts than by geographic relationships or any ecological condition, and the corollary of this, which is that the distribution of the parasites may therefore often have a valuable significance as to the genetic relationships of animals whose genealogic affinities are in process of ascertainment, and in the light of the facts of distribution for the mammal-infesting Mallophaga and Anoplura as just set out in Part ii of this paper. I hardly need do more, in conclusion, than to point out that the distribution conditions exhibited by the mammal parasites, even in the face of the meagre knowledge that we yet have of the mammal-infesting forms, clearly, on the whole, confirm this thesis. In fact, considering how few mammal-infesting parasite species we yet know, it is surprising how repeatedly the commonness of parasite species to two or more related, although geographically well separated, host species, is illustrated. All through the order from Marsupials to Quadrumana this condition is again and again exemplified. I am then, naturally, made more certain of the essential truth of the thesis, and can the more strongly recommend the attention of systematic zoologists to that practical application of it, which I have stated in the form of a corollary."

My personal connection with this subject dates from 1911, when, after about a year's study of Mallophaga, I read a paper before the Sydney University Science Society upon the possible value of these parasites in determining bird affinities. The manuscript of this paper has been lost, but an abstract was published in the

annual report of the Society for 1911-12, which I quote to show that I had already arrived at some definite conclusions in advance of, and independently of, Kellogg:—

"Wednesday, 16th August (1911).—Held in the Geology Theatre, the President in the chair. L. Harrison read a paper, illustrated with lantern-slides, on "The Taxonomic Value of Certain Parasites." The parasites referred to are the biting lice (Mallophaga) found upon birds or mammals. Owing to both environment and food remaining unchanged through the centuries, these insects have not differentiated as fast as their hosts, and afford indications of original relationship between birds that have diverged widely from parent stock. Though birds can be divided into good natural groups, the relationships between these groups have not, and cannot, be satisfactorily determined on anatomy alone. So any line of investigation that is likely to aid the solution of bird phylogeny deserves consideration. Some evidence is afforded confirming parts of existing classifications. Among other results, a study of the Mallophaga would suggest the inclusion of the penguins with the fowls, pigeons, and tinamous, a relationship that has never before been suggested. Such results could, of course, only be put forward as suggestions to the morphologist. A preliminary examination, however, of this group of parasites, certainly suggests that more complete knowledge will afford valuable clues towards the solution of bird taxonomy."

In 1914 I published a general statement of the host-parasite relation in Mallophaga repeating the suggestion as to the position of the Sphesciformes, and including *Opisthocomus* in the same grouping (1914, p. 10). I also discussed the genetic connection of the struthious birds. In 1915 I discussed the parasites of the New Zealand kiwis (*Apteryx* spp.), and produced evidence to show that these were more nearly related to the Ralli than to the other struthious birds. Incidentally I produced evidence that the jacanas were ralline rather than limicoline. In the same year I was invited to open a discussion before Section D of the British Association for the Advancement of Science on the general question of host-parasite relations, an abstract of my address being printed in the *Proceedings* for the year. In the following year (1916) I was asked to address the British Ornithologists' Club, and this address appeared in full in *The Ibis*, and in abstract, with an abstract of the discussion, in the *Bulletin* of the Club. In this address I propounded a classification of the petrels based entirely upon their Mallophagan parasites. More recently I have made use of lice and of other groups of parasites both for phyletic and for zoogeographical purposes, statements of which appear in due course below.

The Chairman of the meeting at which I read my first paper in 1911 was Mr. (later Professor) S. J. Johnston. He told me upon that occasion that he proposed to test my ideas with regard to trematodes and cestodes. He subsequently wrote three short papers, which are discussed below.

G. F. Ferris, pupil of, collaborator with and successor to Kellogg at Stanford, naturally imbibed his teacher's ideas, and has made some contributions to the subject which will be discussed when I deal with lice later on.

Metcalf (1921) was, so far as I am aware, the next independent discoverer of the value of the host-parasite method, being led to it by his investigations of the Opalinid parasites of frogs. In a series of subsequent papers he has based the broadest possible conclusions, both phyletic and zoogeographical, upon the distribution of these parasites. We will touch upon his work when dealing with the Protozoa.

Finally Darling's discussion (1921) of hookworm in relation to man is a further example of independent use of the method, and Grobbelaar (1922) has extended S. J. Johnston's discussion of frog trematodes.   Theses reverberations are at last beginning to reach the ear of the general parasitologist, and Dr. Henry B. Ward, in his presidential address to the first annual meeting of the American Society of Parasitologists, writes (1926, p. 236):—"The significance of studies in parasitology is by no means limited to the fields I have been discussing. Such studies have been shown to have a direct bearing in individual cases on problems of pure science, such as phylogenetic relationships, distribution and the origin of the parasites and their hosts."

He mentions the work of Kellogg, Metcalf and Darling. This brief historical discussion indicates that the same conclusions have been reached, for the most part quite independently of one another, by a number of workers upon various groups of parasites. This unanimity can mean but one thing, namely that the host-parasite relation is a general principle, and is capable of wide application when parasites are better known. I shall now proceed to consider this relation in some selected groups of parasites.

iii.—*The Host-parasite Relation in Protozoa.*

Wenyon (1926, p. 136) writes on the general host-parasite relation in Protozoa as follows:—

"An important feature of parasitism is the specificity of any particular parasite for its host. It is found in nature that some parasites are unable to live in any other host than the one in which they naturally occur. This undoubtedly depends upon the peculiarity of the body fluids of these animals. Some parasites have become so specialized that they cannot survive in any other fluid than the one to which they have become accustomed. Very frequently, however, a particular parasite is able to live in hosts which are nearly related, the fluids of which may be presumed to differ only slightly from one another. Thus *Plasmodium vivax*, which causes benign tertian malaria, cannot survive in any other vertebrate host than man, though Mesnil and Roubaud (1920) have shown that it may multiply for a short period in the chimpanzee. Other parasites are much less specific, for many of the pathogenic trypanosomes can develop in small rodents, which under natural conditions are never infected by them. In such cases it seems probable that quite apart from the suitability of the fluid of a host, the rapidity with which a host can develop antibodies, is the determining factor as to whether a parasite can establish itself or not. Instances are known in which it is only after many attempts to introduce a parasite into a host that success is at last attained. An instance of this is quoted below (p. 576), where Watson, attempting to isolate a strain of *Trypanosoma equiperdum* from horses in laboratory animals, only succeeded in one after inoculating over 600 animals. The infection, once established, was then readily inoculated from one animal to another. It is evident that here the fluids of the animal which gave a successful result differed from those in which inoculation had failed, or that amongst the organisms injected on the successful occasion there happened to be a few which found the environment congenial and were able to resist the antibodies developed. The fact that subsequent subinoculations were easily carried out seems to suggest that the explanation is to be found in the parasites themselves. Not infrequently an animal which has acquired an infection will free itself, after which it is found to be immune to further inoculations. On the other hand, it has been shown

that in some cases, when an infection has disappeared or has been much reduced, further inoculations of the same organism may bring about a superimposed infection which may be more severe than that first produced. Such an instance has been described by Nöller (1917) in the case of frogs infected with *Trypanosoma rotatorium.*

"It may be stated as a general rule that the specificity of parasitic Protozoa for their particular hosts is much more marked than is the case with vegetable parasites, such as bacteria, yeasts and allied organisms. It often happens that a parasite in one host may be morphologically indistinguishable from one in another. yet experimentally it is impossible to produce cross-infections. Whether such biological races are to be regarded as distinct species or not is a problem which still requires solution. From the strictly zoological point of view they should be regarded as belonging to one."

Despite the generally recognized specificity of protozoan parasites, only one group has been studied from the point of view of host affinities and migrations. The very interesting symbiosis between termites and their flagellate parasites, in which Cleveland .(1923) has shown that the flagellates are essential to the continued existence of their hosts, since the parasites alone are able to digest the cellulose of the wood upon which termites feed and to produce substances assimilable by their hosts, indicates a very ancient history of parasitism. Termites and flagellates must have evolved *pari passu* to have reached the present complex condition of interaction. It occurred to me when I first read of this relation that the phenomenon may have a wide general application amongst plant-feeding animals. The striking ciliate and flagellate faunas of the paunch of ruminants, for example, may well prove to have a similar function in aiding the digestion of the cellulose and silica of their hosts' food. Studies have not yet, however, been undertaken along these lines, but I have little doubt that, when they are, there will be a useful crop of by-products in the form of indications of host relationships, etc. I do not intend to traverse the groups of parasitic Protozoa, but will content myself with quoting Metcalf's work (1923, 1923a) on the Opalinid ciliates parasitic (commensal) in frogs, since his comprehensive study indicates that similar results may be expected from the careful examination of other parasitic groups.

Metcalf divides the family Opalinidae into two subfamilies, Protoopalininae possessing two nuclei, and Opalininae, comprising multinucleated forms, of which the former is more primitive. This contains two genera, *Protoopalina* (which is divisible into nine subgeneric divisions) and *Zelleriella.* The more specialized subfamily also includes two genera, *Cepedea* and *Opalina*, the latter of which is further divided into two sections, *Opalinae latae* and *O. angustae.* He is of opinion "that *Zelleriella* arose in tropical America from *Protoopalina*; that *Cepedea* evolved from *Protoopalina* probably in southern Asia; that *Opalina* (broad form) was derived from *Cepedea*, apparently in· Euro-Asia; that the *Opalinae angustae* arose in south-western North America or in Central America when Hylids, coming north from South America, first met Bufos and Ranas bearing broad *Opalinae*, adopted these parasites and changed them to the narrow form" (1923a, p. 393). To quote the full evidence and argument for the above conclusions would take too much space, but we may accept them provisionally as those of the worker most competent to judge. Upon this basis Metcalf discusses the whole broad question of the origin and distribution of the Anura.

What value has such a discussion? Noble (1925) and Dunn (1925), both competent herpetologists, have pooh-poohed it rather contemptuously, and I (1926) have made some reply to their criticisms as far as the Australasian region is concerned. Metcalf has suffered from the usual pitfalls which everywhere beset the path of the generalizer, once he leaves the safe preserve of the group he knows thoroughly. Thus the so-called Bufonids of Australia are not Bufonids at all, but toothless Leptodactylids; there is no Gastrophrynid, nor any frog at all, in Samoa; the record for the Australian *Limnodynastes peroni* in the New Hebrides is erroneous, and is apparently due to a collection of Australian origin having reached the British Museum incorrectly labelled, since other Australian animals have also been wrongly recorded from Erromanga; and finally the position of the New Zealand *Liopelma* is still in doubt. It is pretty certainly a Leptodactylid, but Noble has recently (1922) reaffirmed its status as a Discoglossid. If the data collected from other regions contain similar errors (and I am aware of some) it is small wonder that the generalizer meets with difficulties, and may announce conclusions which are open to criticism.

It would be out of place for me to attempt to follow or to summarize the whole of Metcalf's conclusions as to the past and present distribution of frogs, which he bases upon a study of their Opalinid parasites. I shall, however, briefly consider such of his views as have a bearing upon Australian zoogeography. Australian frogs, if we leave out of consideration four recent immigrants into North Queensland, belong to the families Leptodactylidae and Hylidae.

The Leptodactylidae are parasitized by the Opalinid genus *Zelleriella*, both in Australia and in South America. A few species of *Zelleriella* have apparently pushed up into North America, where they have infested frogs other than Leptodactylids, but the genus is confined to Australia and America. After citing the common possession of this genus of parasite by both Australian and South American Leptodactylids as conclusive evidence against the possibility of convergent development of the two host groups, Metcalf writes (1923, p. 330) :—

"It would perhaps be conceivable, though difficult to believe, that the Australian Leptodactylids may have evolved independently of the South American forms now classed in this family. But it is hardly conceivable that almost identical internal parasites were evolved also independently in the two groups of hosts. *Zelleriella* is a very compact genus morphologically, so compact that subdivision into valid species is difficult. The Australian *Z. binucleata* and some American Zelleriellas are especially similar. There seems no escape from the conclusion that the Leptodactylids of America and Australia, and their parasites as well, arose in some one region and spread to their present localities. The evidence for an Antarctic land connection between South America and Australia is greatly strengthened by the data *Zelleriella* and the Leptodactylidae present. Indeed the evidence seems conclusive. . . . . It seems in agreement with the data at present known to suppose that a great continental mass existed in the Southern Hemisphere up into Miocene times, and that upon this continent, including Australasia and southern South America, there were Leptodactylids which had *Zelleriella* parasitic in them. *Bufo* was not in this Antarctic fauna."

The Hylidæ are most numerous in South America, dwindle in North America, and are represented in Palaearctica by races of a single species with North American affinities. Elsewhere they occur only in Australia, extending northwards to the Moluccas and the more eastern of the Lesser Sundas. They are absent from South Eastern Asia, which offers an environment essentially suited to

them. Concerning their parasites Metcalf writes (1923*a*, p. 392):—"The Opalinid parasites of the Euro-Asian Hylids, so far as known, are of a modern subgenus (*Opalinae angustae*, evolved, apparently, in the Pliocene), are of North American origin, and are utterly different from any Opalinids known in Australasia. *Opalina obtrigona* was the Opalinid found in all the infected Hylas from Euro-Asia. This is perhaps the most modern of all the Opalinidae. The Australian Hylids, on the other hand, have been found to carry Opalinids only of the most archaic genus, *Protoopalina*, a genus of world-wide distribution. The Euro-Asian Hylid parasite, *Opalina obtrigona*, is almost identical with the North American species *O. obtrigonoidea*, which occurs in several North American genera, including Hylids of five species."

Metcalf's conclusions from parasitological evidence thus support the view generally held by Australian zoogeographers that the Hylids and Leptodactylids entered Australia from the south, and tend to refute that put forward by Matthew (1915), Noble (1922, 1925) and others that these families reached Australia from the north. They also serve to refute Noble's claim that the Australian Leptodactylids are genetically continuous with Asiatic Bufonids. Since only a small part of Metcalf's total conclusions has been discussed, it seems reasonable to hope that a detailed study of other groups of parasitic Protozoa with regard to the affinities and distribution of their hosts will yield results of equal importance.

It should be mentioned, however, that Opalinids are commensals, not true parasites, and appear to be viable in any frogs to which they have access. They are, therefore, less useful than Protozoa which have a strict host-parasite specificity. But inferences such as that drawn from the distribution of the genus *Zelleriella* seem well justified. The genus is absent from the Palaearctic, Oriental and Ethiopian regions, and it may fairly be argued that the ancestors of the existing Leptodactylids have never existed in these regions. The study of host-parasite specificity is in its infancy, but Andrews (1927) after careful cross-infection experiments with coccidiosis in mammals, concludes:—"The coccidia of mammals seem to be strictly host-specific parasites, as judged by cross-infectivity experiments on cats, dogs, rabbits, skunks, opossums, pigs, and prairie-dogs."

### iv.—*The Host-parasite Relation in the Temnocephaloidea.*

The Temnocephaloidea are commonly considered as an order of monogenetic Trematodes, but their true affinities appear to lie with the Rhabdocoele Turbellaria. They are somewhat leech-like creatures, with a large muscular posterior sucker, and a series of adhesive tentacles, varying in number, usually arranged in a single row at the anterior end. They have a preponderant obligate association with fresh-water Decapods, but in South America species occur upon fresh-water tortoises and a fresh-water mollusc. A couple of species have been described from fish in the Oriental region, but my colleague Miss Lucy M. Wood, who has for some time been working on the group, will not allow that these are Temnocephaloids. Their normal habitat appears to be upon the external surface or in the gill-chambers of fresh-water crayfishes (Mexico, South America, New Zealand, Australia with New Guinea, Madagascar); but they also occur on fresh-water crabs (South America, New Guinea, Philippines) and shrimps (South America, Australia) and upon the curious archaic Isopod, *Phreatoicopsis*, in Australia. The group is thus confined to the southern hemisphere, save for the anomalous occurrence of a species in Mexico, and a second in the Philippines.

Temnocephala mexicana occurs upon the Potamobiid crayfish *Cambarus digneti* in Mexico, and affords the only known instance of a Temnocephaloid upon the northern crayfishes. This species appears obviously to be a recent derivative from South America. *T. semperi* occurs on *Telphusa* sp. of Sunda, Philippines, and is an extension, like its host, from the Australasian region upon a well-known migration route (Merrill, 1926; Harrison, 1928a). The Temnocephaloidea are confined to fresh waters, and show no evidence of marine origin. Their distribution in South America, New Zealand, Australia and Madagascar is coincident with that of the Parastacid crayfishes. I have cited this example (1926, p. 379-382) as affording positive evidence of the connection in past time of these four widely-separated southern land-masses. My argument is further strengthened by a consideration of the distribution of the fresh-water Histriobdellids discussed below (p. xxv). We have here a host-group, itself confined to four southern land-masses, associated with two parasitic groups which are totally unrelated. The first parasitic group is associated with crayfish hosts in all four countries; the second with crayfish in two, and with another fresh-water Decapod in a third, and may yet be found upon crayfish both in New Zealand and South America. When we add to this the circumstance that two species of Phreodrilid oligochaetes are found ectoparasitic in the eye-sockets of Australian crayfish, and that the Phreodrilidae are confined to the extreme south of Africa, Australia and South America, and to the widely separated islands of the sub-antarctic zone, we have a chain of data which, to me, appears to oppose an insuperable obstacle to any hypothesis for the northern dispersal of the southern crayfishes. As I mention below, they appear to me to have been derived at one time and in one place from marine ancestors, and to have achieved their present dispersal by migrations over land routes. This implies either land bridges, or the shattering of an original southern continental mass, as suggested by Wegener. Of the two, Wegener's hypothesis seems the more probable.

The Temnocephaloidea are richest in genera and species in Australia, South America coming next, but with the genus *Temnocephala* only, of which genus New Zealand has two species and Madagascar one. This last will be made the type of a new genus. The group has certainly undergone radiation in Australia, but, when Miss Wood's studies are completed, they will afford some indication that the Australian Temnocephaloids were derived with those of New Zealand, and must have entered from the south. This would imply a derivation from Antarctica, which may have been a centre of radiation for Temnocephaloids. Much depends upon the final determination of the status of the Madagascar species, specimens of which have recently been received for investigation. I must not here anticipate Miss Wood's results, but she is fairly confident that she will be able to do a good deal towards tracing the migrations of the crayfishes themselves when she has completed her survey of their Temnocephaloid parasites. From the viewpoints of both zoogeography and parasitology, the Temnocephaloidea are an important and interesting group.

v.—*The Host-parasite Relation in Trematoda.*

Stiles and Hassall's Index Catalogue of Trematodes (1908) is now twenty years old, and is thus to a certain extent unreliable as a guide to anyone not versed in the systematics of Trematoda. On this account I do not propose to attempt any close investigation of the host-parasite relation in this group, but will rely upon the statements made by S. J. Johnston (1912, 1913, 1914), supplemented

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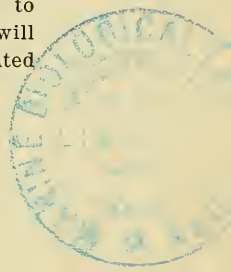
by Grobbelaar's excellent paper (1922) extending Johnston's discussion of the relation between the distribution of frog trematodes and their hosts.

Johnston's analysis (1913, p. 272-3) of the frog trematodes of Europe, America, Australia and Asia shows that in the subfamily Haplometrinae species of *Pneumonoeces* occur in the lungs of frogs of all four continents; and species of *Halipegus* in the buccal cavity of frogs in Europe, America and Asia. In the subfamily Plagiorchinae closely related species occur in the intestine of frogs of Europe, America and Australia, but have not so far been recorded from Asia. Other intestinal parasites belonging to the subfamilies Brachycoelinae and Pleurogenetinae occur in the frogs of all four continents. Bladder parasites belonging to the subfamilies Gorgoderinae and Polystominae are not recorded from Asia, but occur in the remaining three continents, as do rectal parasites of the genus *Diplodiscus* (Paramphistomidae). Grobbelaar (1922) has brought Johnston's work up to date, and has shown that the same relations hold for African frogs. Johnston (*loc. cit.*, p. 276) accounts for this remarkable condition as follows:—

"When the amphibian ancestors of the frogs appeared in the world—long before the frogs themselves—they became . . . infected with a number of forms of trematodes. These trematodes probably much more closely resembled the present day trematode parasites of frogs than did those amphibian ancestors the frogs of to-day, for the worms by that time were an old group of animals, and less likely than the newly evolved amphibian to be very plastic. And, not only so, but their mode of life rendered them less likely to be rapidly affected by environmental changes than free-living animals. As the descendants of those early amphibians dispersed to the four corners of the earth, they took their parasites with them, and while the old amphibians have become altered very considerably, the parasites have probably altered only a little, but still have altered; so that we find the old types of Pneumonoeces, that affected to live in the lungs, represented by a dozen or so species scattered over various parts of the earth. And so on with the others, *e.g.* Gorgoderinae, Brachycoelinae, etc.".

Johnston proceeds to a statement that the trematodes of Australian frogs find their nearest relatives in those of Asiatic frogs, and Grobbelaar accepts this statement. This is against the weight of the zoogeographical evidence drawn from the frogs themselves, and is also against the conclusions drawn by Metcalf from his studies of the Opalinid parasites of frogs, but would accord with the views of Matthew, Noble and others concerning the radiation of frogs from a northern centre of dispersal. It must be borne in mind, however, that Johnston knew only six species of frog trematodes from Asia, that only a small portion of this fauna has been described for Australia, and that nothing whatever was known of the frog trematodes of South America. So we have here an interesting test case for future judgment. When the frog trematodes of Asia, Australia and South America are better known, it will be possible to determine whether those of Australia are more nearly related to the Asiatic or to the South American fauna, a matter which will largely assist in determining the affinities of the frogs themselves. I myself have the utmost confidence, derived from many collateral lines of evidence, that ultimately the closest affinities of Australian frog trematodes will be found to lie with those of South American frogs.

In the same paper (p. 278) Johnston makes brief mention of a few other trematode relationships; the various species of *Scaphanocephalus* from sea eagles in different regions are very closely related to one another, as also are those of

Bilharziella from seagulls and of *Hemistomum* from herons; two species of *Harmostomum* from the Australian marsupials *Dasyurus* and *Perameles* are so closely related to *H. opisthotrias* Lutz from an American *Didelphys* that they must be considered as derived from common ancestors; and finally the flukes from an Australian marsupial and monotreme comprise a subfamily intermediate between the Fasciolinae of higher mammals and the Psilostominae of reptiles and birds.

In 1914 Johnston extended his studies to Australian Trematodes and Cestodes in general; and in 1916 devoted considerable space to a discussion of the relations of the trematodes of Australian birds with those of birds elsewhere. He concludes (1916, p. 254):—

"Of the fifty-one trematodes of Australian birds mentioned in the foregoing table, thirty find their nearest relatives in trematodes parasitic in birds of the same family, ten in birds of a closely related family, and seven in birds which cannot be considered closely related to the Australian bird-hosts, while three are so constituted that they do not seem to have any near relatives amongst known trematodes.

"In the case of the first group and perhaps also of the second, it may be considered that the pairs of related trematodes have been derived from common ancestors, and also that their hosts have been derived from common ancestors, and that the ancestors of the trematodes were parasitic in those of the birds. For instance, *Holostomum hillii* and *H. eraticum*, two closely related species of *Holostomum*, are parasitic in various species of *Larus*. These sea-gulls are apparently derived from common ancestors in which the species of trematode that gave rise to *H. hillii* and *H. eraticum* was parasitic. As the original *Larus* spread over the earth till, in the course of time, it attained the present very wide distribution of the genus, by the acquisition of different characters it became split up into a number of species. Evolutionary agencies were at the same time working on the trematodes which accompanied the birds, and one group eventually became separable from another as a distinct species.

"The want of relationship between the hosts in the case of the seven pairs in the third group, may be explained on the supposition that in the one case or the other the parasite has been acquired by the bird much more recently."

The evidence brought forward by Johnston proves conclusively, I think, that there is a very marked specificity in the relations of trematode parasites to their hosts. Anomalous distributions occur, as in almost any other group of parasites, and these may be due to comparatively recent acquirements which are not natural to the hosts from which they have been recorded. But it is also possible that an extended knowledge of the trematode parasites of vertebrates, of which only a small portion is known, will clear up many of these apparent anomalies, by indicating more precisely the real affinities of the parasites. Trematodes seem likely to be of very real value in affording light upon the relationships and migrations of their host groups.

vi.—*The Host-parasite Relation in Cestoda.*

Although it was in this group that Zschokke indicated for the first time, so far as I am aware, the value of parasites in the determination of host affinities, it nevertheless does not appear to offer, in the light of present knowledge, much useful data for this purpose. Zschokke based his statement upon the common possession by marsupials in America and Australia of cestodes of the genus *Linstowia*. *Linstowia echidnae*, however, is recorded from both a monotreme

and a marsupial in Australia, and these have no close affinity. Moreover, the subfamily Linstowinae includes five genera: *Inermicapsifer*, confined to the mammalian genus *Procavia*; *Linstowia*, which is confined to marsupials and a monotreme, save for a species described from Beddard from the lemuroid *Nycticebus*; *Multicapsiferina*, found in five genera of mammals ranging from rodents to monkeys; *Oochoristica*, which is more characteristic of reptiles, but which is found in marsupials in America and Australia, but is also found in badgers, new world monkeys, armadillos and anteaters; and *Palaia*, found only in reptiles. One might be tempted to suppose that the subfamily is a very ancient one, confined to reptiles and primitive mammals, but an example such as is afforded by *Oochoristica megastoma*, which is recorded from eleven species of new world monkeys, belonging to seven genera, vitiates such a suggestion.

The following data concerning the cestodes of Australian marsupials are taken from Meggitt (1924). *Linstowia* and *Oochoristica* have already been discussed. *Moniezia*, characteristic of ungulates, has a species, *M. bipapillosa*, in the wombat, *Phascolomys mitchelli*. *Cittotaenia*, chiefly found in rodents, has a species in the echidna, and a second in a wallaby, *Lagorchestes conspicillatus*. *Progamotaenia*, *Hepatotaenia*, *Bancroftiella* and *Dasyurotaenia* are confined to Australian marsupials, and their precise affinities are not known. *Pavoniella* has a species in *Macropus brunii*, and occurs elsewhere in two rodents and two pangolins of the genus *Manis*. A species of *Hymenolepis*, probably characteristic of rodents but widely distributed in mammals in general, is recorded from *Perameles macrura*. Species of *Bertiella* occur in phytophagous marsupials of the genera *Phalanger*, *Phalangista*, *Phascolarctos* and *Pseudochirus*, as well as in monkeys, lemurs, and four species of rodents.

Such distributions are frankly incomprehensible. It may be that not enough cestodes are known, or that an adequate means of natural classification has not been attained. But even granting this, the Cestoda appear to exhibit a much greater degree of viability than is shown by the Trematoda. Nevertheless there are some facts which appear to indicate that a host-parasite relation does underlie the apparent confusion. Thus Johnston (1914, p. 243) notes that the same tapeworm, *Davainea struthionis*, is found in both the African ostrich and the American rhea, while a closely related form, *D. australis*, is found in the Australian emu. And many genera do show restriction to a limited host group.

vii.—*The Host-parasite Relation in Nematodes.*

As a basis for the examination of this group, I have used Stiles and Hassall's Index-Catalogue (1920), together with Cram's recent study (1927) of three Nematode suborders parasitizing birds. It must be confessed at the outset that Nematodes do not appear to display any great degree of specificity towards their hosts. Many of the larger genera are cosmopolitan in distribution, and are spread over a startling variety of host groups. On the other hand there are many monotypic genera, or genera with a limited number of species from the same host or host group, from which I can read no meaning, since I am not familiar with the systematics of these parasites, but which might mean more to a specialist in them. There are, moreover, a number of factors which militate against a clear understanding of the relations of Nematodes to their hosts, in the present state of knowledge. Only a small fraction of the group is known; life histories are very largely unknown; distribution may often be determined by that of unknown intermediate hosts; for these, when better known, a more specific host-parasite

relation may hold; the lists of species are clogged with old records, the precise status of which is not known, as well as with misidentifications by more recent workers; and finally the general problem of the viability of Nematode species is far from being fully solved.

A casual survey of Nematode genera appears to indicate that they may be divided roughly into five categories as follows:—

(i) *Genera with species which seem to be able to parasitize any animal group whatever.*

The genus *Heterakis*, for example, is found in various fishes, in frogs and salamanders, in most groups of reptiles, in almost every order of birds, and in such diverse mammals as monkeys, tarsiers, the agouti and the guinea-pig. *H. gallinae* occurs in the bird genera *Anas, Tadorna, Anser, Chenopsis; Ceriornis, Chrysolophus, Colinus, Coturnix, Cupidonia, Gallus, Crossoptilon, Lagopus, Meleagris, Numida, Ortyx, Pavo, Perdix, Phasianus, Bonasa, Tetrao*; and finally *Otis* and *Corvus*; that is to say, in four anseriform and sixteen galliform genera, finishing up with two bustards and a crow. The only conclusion to be drawn from such a distribution is that the species must be viable in almost any kind of bird host, although it must be remembered that the host genera are all commonly kept in zoological gardens, occupying in succession the same enclosures, so that although the parasite may be viable in all these hosts, it may not be a natural parasite of many of them. But a glance down the list of bird-infesting species of *Heterakis* does not offer much promise of definite specificity. Sixteen species are recorded by Cram as having a single host, five as having two closely related hosts (congeneric in three) and two as having two unrelated hosts; while four are found in numerous pheasant genera, and one in thirteen anserines and an owl. A similar history attaches to most of the larger genera, such as *Oxyuris, Physaloptera, Spiroptera* and many more.

(ii) *Genera with species which are confined to predatory groups and their prey.*

This category covers a relation which is very general amongst helminth parasites, especially those which require an intermediate host in their life history. In such organisms the intermediate is the prey of the final host, and harbours some kind of larval stage of the parasite found in its adult form in the final host. Thus in *Dispharynx spiralis* the infective larval stage is found in the terrestrial isopod *Porcellio*, and the adult occurs in a variety of ground-feeding birds, chiefly galliform. The infective larvae of *Echinuria uncinata* occur in the "water-flea," *Daphnia*, and the final stages in aquatic anseriform birds. *Echinorhynchus strumosus* has its larval stages in various fishes, and occurs in the adult form in seals and cetaceans, and so on.

(iii) *Genera either themselves confined, or having species confined, to fairly limited host groups.*

Epomidiostomum is confined to anseriform birds, *Codiostomum* to three species of ostriches in Africa, and *Deletrocephalus* to rheas in South America, *Acanthocheilus* to sharks, *Belascaris* to cats and dogs, *Cylichnostomum* to equidae, *Dictyocaulus, Onchocerca* and *Ostertagia* to ungulates, *Kalicephalus* to snakes, *Prosthecosacter* to cetaceans. Further genera might be cited, but these are sufficient to indicate some kind of obligate relationship between hosts and parasites, the precise nature of which cannot at present be stated.

Amongst species, *Heterakis alata* is found in two species of tinamous in Brazil, as also is *H. valvata; H. hamulus* occurs in two species of peacocks, and *H.*

papillosa in two species of bustards. *Ascaridia hermaphrodita* has been found in nineteen species of South American parrots, belonging to four genera; *A. columbae* in thirteen species of pigeons has a cosmopolitan distribution; *A. cristata* and *A. stroma* are confined to cranes; while *A. numidae* occurs in three species of guinea fowls in Africa. *Viguiera euryoptera* is found in four species of shrikes of the genus *Lanius*, *Acuaria quadriloba* in woodpeckers of several genera in Europe and U.S.A., *Chevreuxia revoluta* in two species of *Himantopus*, and similar limited distributions might be quoted almost *ad infinitum*.

(iv) *Genera which either as a whole or in some of their species appear to afford indications of the underlying genetic affinity of their hosts.*

Few nematode genera fill this condition, but two striking examples may be quoted. The genus *Echinonema* contains two species only, one of which occurs in the marsupial *Perameles obesula* in Australia, the other in the marsupial *Didelphys azarae* in South America. The genetic affinity of the American with the Australian marsupials is confirmed by four separate categories of common parasites, nematode, trematode, cestode and mallophagan. The second example is afforded by the two genera which compose the tribe Deletrocephaleae of the sub-family Strongylinae. These are *Codiostomum*, with a single species found in three species of ostriches in Africa, and *Deletrocephalus*, with a single species occurring in *Rhea americana* of South America. Despite the view generally held by ornithologists that ostriches and rheas are not closely connected, a study of their parasites affords convincing evidence that they are.

These two examples, taken in conjunction with some of those quoted in the preceding section, suffice to show that, underlying the apparent confusion and disorder of nematode distribution, there are traces of a specific host-parasite relation such as is exhibited by most obligate parasites.

(v) *Genera and species the distribution of which is so extraordinarily mixed that no satisfactory conclusions can be drawn from them.*

This fifth category partly overlaps the first, but is meant to apply to conditions other than general viability. Thus the genus *Ornithostrongylus* has a species in the domestic pigeon in Australia and U.S.A., a second in a Brazilian *Leptotila*, a third in the African ostrich, while the fourth and fifth occur in the European bustard and grouse respectively. Even if it be granted that there are many more species to be discovered, no sense can be read into such a distribution, and one suspects at once that the genus is not a natural one. This is Miss Cram's opinion, and she writes (1927, p. 12):—"The pattern of the bursal rays is so divergent in the species included by Travassos in this genus as to raise a doubt as to whether all these species are congeneric."

The genus *Aspidodera* contains five species, two of which occur in marsupials of the genus *Didelphys*, and two in armadilloes belonging to several genera. The fifth occurs in both opossum and armadilloes. Such a distribution cannot be read as indicating genetic affinity, and it may be that some common food factor will ultimately explain it.

In the present state of knowledge it does not appear that nematodes can afford much help in unravelling the affinities of their hosts. But a better knowledge may reveal a different state of affairs. The chief hindrance seems to lie in the very general viability of nematodes. Thus the common gape-worm, *Syngamus trachea*, has achieved an almost cosmopolitan distribution in a wide variety of hosts. Yet Cram (1927, p. 37) is able to show that it is a natural parasite of the

North American turkey, from which it has become transferred to all its other hosts. Bound up with this is the question of the reaction of the parasite to conditions obtaining in a new host, which tends to produce variations which may or may not be of specific value. One need but recall the interminable discussions about the status of the larger species of *Ascaris* found in the domestic animals and man.

Sandground (1926) has made a careful study of this aspect in the genus *Strongyloides*. He writes (p. 66):—"In summing up the consideration of speciation in this genus, I may repeat that the incompleteness of certain records at present permits us to recognize representatives of the genus in mammals only. The parasite in no instance has undergone any fundamental morphological differentiation which can be correlated with physiological adaptation toward special environmental conditions in a particular host species. The most outstanding differences that are recognized in our present conception of specific distinction in the parasitic generation is that of size, but the relation that obtains between a parasite and its hosts must not be disregarded in the evaluation of this character. There appears to be no single character by means of which a specimen may be relegated to its specific position; on the other hand it is, I think, possible to make a determination in a considerable number of individuals if a number of characters representing the different stages in the life-history of the form be jointly considered."

After remarking that some nematodes can successfully invade many hosts, while others are restricted in habit, Sandground proceeds to a general discussion of the phenomena of specificity in nematodes, for quoting which I make no apology, since it embodies the opinions of an expert worker in the group, and has therefore a far greater value than my own. He writes (*loc. cit.*, pp. 68-69):—

"Relatively little attention has been given until very recent times to the study of specificity among nematodes but in the application of parasitology to control work, it may become a subject of no little importance.

"Among nematode parasites of plants, there are some . . . which are polyphagous in their habits. When attempts are made to transfer some of these forms to other host plants, known to be attacked by the same parasite in nature, success does not always follow. . . It seems that the restriction of a population of parasites to a particular host species for a great number of generations leads to a special adaptation towards this species and a corresponding loss of adaptability towards other hosts. This loss may only be temporary but if the parasite be restricted for a sufficient number of generations the probabilities are that the loss will be permanent. The mechanism of this host restriction may be of the nature of a physiological ability to utilize food of only a particular chemical constitution. Should no somatic changes occur in the structure of the parasite during this time, an inability to establish it in its original host under experimental conditions would lead to its being considered as a biological variety but should morphological adaptations develop concomitantly with the development of a host specificity, the parasite would come to be recognized as specifically distinct from its parent stock.

"The situation among nematode parasites of animals is, I believe, closely analogous to that which obtains among nematode plant parasites. The development of structural differences in certain groups of nematodes which parasitize different hosts is sometimes of a low order. The degree in which it occurs may

depend upon several factors, such as the intrinsic plasticity of the parasite, the extent to which the change in environment in a new host calls for special adaptations, an evolution time factor, as well as upon other factors of a more obscure or less intelligible nature. Several intermediate gradations may be recognized in the evolution of a complete specificity of a parasite towards its definitive host. When embryonated eggs of several species of Ascaris are fed to abnormal hosts, the larvae which hatch from the eggs undergo the normal migration through the vascular system and lungs but when they return to the intestine, they are unable to establish themselves and are passed out of the body. The parasite shows different degrees of adaptation to different host animals. In some animals (rats, guinea pigs, etc.) *Ascaris lumbricoides* is eliminated at an early stage, while in other animals (sheep, goats) the larvae can develop to a stage approaching maturity before they are out of the intestine. There are many who recognize a specific distinction between parasites which although morphologically indistinguishable appear to possess a high order of host specificity; thus for example *Ascaris lumbricoides* and *A. suum*. Although this procedure may not be warranted from the point of view of the systematist, from the standpoint of applied parasitology it is probably justifiable. The ability of a parasite to proceed to a certain stage in its development in an abnormal host may be further illustrated by the example of the human hookworm, *Ancylostoma duodenale*, which according to Looss and other observers is able to develop in young dogs almost to the mature stage before passing out of the abnormal host. In *Strongyloides* a most advanced condition is encountered; certain species, as will be shown later, develop to maturity in certain abnormal hosts and proceed to produce young but after a shorter or longer time the prolificity of reproduction gradually diminishes and eventually ceases, presumably with the death of the parasites."

Sandground follows with an account of some infection experiments, the most interesting of which is that with *Strongyloides fülleborni*, a common parasite of old world monkeys, including anthropoids. He did not succeed in inducing infections in dogs, cats or rats, but produced a small infection, persisting up to the eighth day, in man. Using *Ateles geoffroyi*, a new world monkey, he was able to secure a few larvae after five and six days, but failed in several attempts to reinfect. He concludes that the old and new world *Strongyloides* are distinct, but these experiments also suggest, though the evidence is slender, the closer affinity of man to the old world monkeys, and the more remote affinity of the genus *Ateles*, which, it is of interest to note, harbours a louse of the genus *Pediculus*, otherwise confined to man and the old world anthropoids.

Finally Darling (1920, 1921), who was a leading authority on hookworm, has actually used the host-parasite relation of the hookworms of man, *Ancylostoma duodenale* and *Necator americanus*, as a basis for some interesting and suggestive speculations as to the interrelations and wanderings of the races of man. After stating (1921, p. 323) that either species is equally viable in any kind of man, he points out that holarctic peoples show a marked predominance of *A. duodenale*, while the predominant parasite in peoples of the Oriental and Ethiopian regions is *N. americanus*, which he found also in uncontaminated Fijians. He suggests that a survey of uncontaminated American Indian communities may indicate the origins of these peoples, and further that it may be possible to revise the ancestral tree of the primates after a study of the host relationships of their respective obligate nematode parasites.

It thus becomes evident, despite the hopeless confusion which the nematodes present to a generalizer not conversant with the group, that, in the hands of experts and after they are better known, they will afford the same kind of evidence of host relationships as do other obligate parasites.

viii.—*The Host-parasite Relation in Histriobdellids.*

The Histriobdellidae are a family of primitive worms which are generally included in the Archiannelida, although they show no very obvious relationships with any other members of this group, and in some respects come nearer to the Trochelminthes. The family is a small one, comprising, so far as is at present known, only five species contained in two genera. These are:—

Histriobdella homari van Beneden, found upon a European marine lobster, *Nephrops norvegicus.*

Stratiodrilus tasmanicus Haswell, found upon the Tasmanian crayfishes, *Astacopsis tasmanicus, A. franklini.*

Stratiodrilus novae-hollandiae Haswell, found upon the Australian crayfish, *Astacopsis serratus.*

Stratiodrilus haswelli Harrison, found upon the Madagascar crayfish, *Astacoides madagascariensis.*

Stratiodrilus platensis Cordero, found upon a fresh-water anomurous crab, *Aeglea laevis,* in Uruguay.

Both genera have an obligate association with the gill filaments of decapods, upon the surface of which they normally live, though whether as parasites or as commensals has not been accurately determined. *Histriobdella,* the more primitive genus, is marine and has been found only in the northern hemisphere. *Stratiodrilus* is found in fresh waters of the southern hemisphere, in land masses as widely separated as South America, Australia and Madagascar, and its characteristic association appears to be with the southern crayfishes of the family Parastacidae, which are distributed in South America, New Zealand, Australia and Madagascar. I have dealt with these in more detail above, when discussing the host-parasite relations of the Temnocephaloidea. I have recently (1928) described and figured the species of *Stratiodrilus* from Madagascar, and figured also the South American species, and have drawn the following conclusions:—

"It seems reasonable to conclude that *Stratiodrilus* comes of marine ancestors, and that it, or an ancestral form of it, lived upon the marine forerunner of the Parastacid crayfishes. The transition to fresh-water conditions must have taken place once, and once only, upon a single land mass, for, even if it be argued that there were several migrations of marine Decapods carrying Histriobdellid parasites from the sea to the fresh waters of widely separated southern lands, these could not have received fresh-water Temnocephaloid parasites, which again must have had common origin on a single land mass. The association of the Parastacid crayfish with two unrelated parasitic groups, one probably of marine origin, the other giving no evidence of such an origin, seems to me to demand conclusively that there should have been land connections between Madagascar, Australia, New Zealand and South America in past time. Wegener gives the most plausible suggestion, and I have discussed this elsewhere (Harrison, 1928a). A difficulty would arise in connection with the absence of crayfishes from Africa, and it must be supposed that Madagascar had no land connection with Africa after it had received its crayfishes from the east."

ix.—*The Host-parasite Relation in Lice.*

Both biting and sucking lice are now included in a single order, Anoplura, following upon the work of Mjöberg, Kellogg and myself. I have further shown (1916) that the sucking lice are an offshoot of the more specialized suborder of biting lice, the Ischnocera. The work of Snodgrass (1896) has indicated quite clearly that the Anoplura as a whole are derived from the Copeognatha. The Anoplura are now divided into three equivalent suborders, Amblycera and Ischnocera comprising the biting lice, and Siphunculata the sucking lice. The interrelations of these are not quite clear. The Amblycera constitute the more generalized type, but show no obvious intergrades towards the Ischnocera, the two suborders being very sharply cut off from one another. My own opinion is that they represent an earlier and a later independent derivation from psocid stock. The Siphunculata are certainly derived from the Ischnocera, and a link in this derivation is certainly provided by the elephant louse, *Haematomyzus*, which is so distinct from either (Harrison, 1919) that it is probably entitled to equivalent subordinal rank.

The more primitive Amblycera are two-clawed (except for the family Gyropidae, in which one claw has become lost) and have the antennae concealed in a fossa beneath the head. The Ischnocera and Siphunculata have the antennae freely exposed laterally, and have but a single functional claw. All Ischnocera save the Trichodectidae, however, exhibit a non-functional second claw, in various stages of reduction, and not connected with the flexing apparatus of the tarsus, which accounts for the usual statement that the Ischnocera are two-clawed. *Haematomyzus*, *Scipio* and *Hybophthirus* amongst the Siphunculata show similar traces of derivation from a two-clawed condition.

The host relations of these major groups are of considerable interest. The Amblycera occur upon birds, upon marsupials both in Australia and in South America, and upon a certain number of rodents in South America only, and not in any other part of the world. Those which occur upon mammals are at present included in three families, the Boopidae on Australian marsupials, the Trimenoponidae upon marsupials and rodents, and the Gyropidae upon rodents in South America. Ferris (1922, p. 76) has discussed this somewhat anomalous distribution as follows:—

"As has been many times pointed out, one of the most interesting problems in connection with the study of these ectoparasites is that of their distribution. This is, at least in part, the problem of the genetic relationships of their hosts. Just how far the two problems are concurrent is the most fascinating aspect of it all. In the case of the South American two-clawed species infesting mammals it is evident that the two problems diverge rather early, at least if we may form any conclusions from the rather scanty amount of information that is available.

"The majority of the two-clawed Mallophaga from mammals have been taken from marsupials in Australia and for these Harrison has named a distinct family the Boopidae. Two of the species herein dealt with are from marsupials, but apparently they find their nearest relatives not in the Australian marsupial-infesting species but in other species from South American rodents. The one consolation for those of us who like to see our theories work as they should is that these two species are apparently referable to the same genus. Of the other three species, one is from members of the rodent family *Lagostomidae*, one from the family *Octodontidae*, and one from the family *Caviidae*. There is at least a

suggestion that here the problem of the distribution of the parasites is in large part geographical.

"A similar situation appears to exist in the case of the Mallophagan family, *Gyropidae*, the members of which occur upon mammals that appear to have little more in common than the circumstance that all are South American."

Ferris's paper, published in England, anticipated by a fortnight one of my own bearing practically the same title published in Australia, in which I wrote (1922, p. 154) as follows:—

"Mallophaga from Australian marsupials are contained in a family, the Boopidae, which finds its closest relations in the Gyropidae, a family found upon certain South American rodents. Certain South American rodents also harbour the two contained species of a third family, the Trimenoponidae. With the exception of these three small groups, all mammalian Mallophaga belong to the widely different family Trichodectidae, which is placed in a distinct super-family.

"Believing as I do that Mallophagan parasites afford valuable indications as to the genetic relationships of their hosts, I have always been puzzled by this distribution. That the marsupials of Australia should not carry the same kinds of parasites as the Eutherian mammals is reasonable enough. But, apart from marsupials, I should have expected all other mammalian Mallophaga to belong to the Trichodectidae. Hence the occurrence of two small, but distinct, families, not upon rodents in general, nor even upon American rodents in general, but on a limited number of South American rodent species, families which showed, moreover, some relationship with the Boopidae, but differed from all other Mallophaga, was difficult to reconcile with my ideas.

"The explanation would appear to be that such Amblyceran Mallophaga as occur on South American rodents have been migrants in the past from the marsupial stock. The new genus which I describe from a South American marsupial must be placed in the Trimenoponidae, but shows marked features of resemblance to the Boopidae, and some points of contact with the Gyropidae. It is, of course, no use trying to base definite conclusions on a single marsupial-infesting species, but it seems likely that, when more information is available concerning the Mallophagan parasites of American rodents and marsupials, the suggestion thrown out here may be upheld. It is also possible that the discovery of further connecting forms will make it advisable to unite these three anomalous groups under one family name."

The additional information contained in Ferris's paper confirms me in my opinion. The marsupial fauna of South America is a dwindling remnant of once dominant forms, as is indicated by the rich deposits of marsupial remains found by Ameghino. *Peramys* and *Caenolestes*, marsupials from which Ferris records two-clawed Mallophaga, are small creatures of rodent-like habit and habitat. Unless it be assumed that these and their like have passed their parasites on to rodents sharing their haunts, we must accept a condition otherwise unprecedented amongst lice, which have no zoogeographical distribution independent of their host groups. That two-clawed Mallophaga are viable on other than their natural hosts is well shown by the large number of records of the taking of *Heterodoxus*, a Boopid genus absolutely characteristic of the Australian marsupial genus *Macropus*, upon dogs, foxes and coyotes in various parts of the world. Paine was so much impressed by this fact that he has stated (1912, p. 361) that this genus is mammal infesting, probably characteristic of dogs.

The Amblycera, then, appear to be natural parasites of birds and marsupials, while the Ischnocera are natural parasites of birds and placental mammals. The Siphunculata are entirely confined to placental mammals. This distribution suggests a very ancient history of parasitism, and, taken with other available data, has led me to the opinion that the Amblycera parasitized birds and marsupials before the placental mammals came into existence, while the Ischnocera and Siphunculata are of later origin than the marsupials themselves. Since, however, the two latter groups have a cosmopolitan distribution upon placentals, they must be practically as ancient as these mammals. Consequently we have a history of parasitism for all three groups which must cover practically the whole period of evolution of their hosts. Since the parasites have not, in general, evolved at so rapid a rate as their hosts, their relationships may be more easily traced, and will in many cases afford suggestive evidence as to host affinities.

I do not intend to discuss the Amblycera in any detail. They are more active than the Ischnocera, tend to wander from the body of the host after death, and seem to be able to live without inconvenience upon other than their natural hosts. In general, however, they display a specific host-parasite relation, and, when better known, will probably prove almost if not quite as useful as the Ischnocera for the purpose of assessing host affinities. Those genera which have been definitely delimited in recent years exhibit precise host relations. The genus *Tetrophthalmus* is confined to pelicans, *Eomenopon* to parrots, *Trochiloecetes* to humming-birds, and so on. Ferris and Uchida are in process of making critical studies of the suborder, and, when these are completed, the results will very certainly lend themselves to a consideration of host relationships.

The Ischnocera, however, are much more valuable from this point of view. They are more diversified in form, exhibit a better range of characters, and show a much higher degree of specificity towards their hosts. This last is very largely due to the fact that they do not leave the body of the host at death, but fix themselves by their mandibles to feathers or hair, and die *in situ*. They may, in consequence, be easily, and for the most part safely, collected from dried skins in museums, and it is of passing interest to note that I have a fairly considerable collection taken from skins collected by the *Challenger*, as well as a few dating back to the voyage of the *Beagle*.

The condition among the Ischnocera is such that the parasites of any host group have a common facies, and are recognizable at sight as coming from a particular host group. I should scarcely be justified in saying that I could name the host group for any Ischnoceran that was submitted to me, since there are some groups of birds with whose Ischnoceran Mallophaga I am not familiar. But for all well-known groups of birds with a wide distribution I could say without hesitation that a given louse came from a crow, a kingfisher, a cuckoo, a parrot, a gannet, a petrel, or such other bird as might be. For those groups which I have studied most intensively I would go even further. For almost all Ischnoceran parasites of the Tubinares, for instance, I could name the actual genus of petrels from which any louse shown me was derived.

There can be no doubt whatever that the Ischnoceran Mallophaga have evolved *pari passu* with their host groups, and that the latter carry their appropriate parasites whether at the pole or the equator. After a number of years of study I am just bringing to conclusion a critical examination of the Ischnocera as a whole, which will involve the diagnosis of upwards of a hundred new genera, and which will exhibit the main lines of evolution within the

group. I do not propose to anticipate here the results of this study, but, although inadequacy of material in certain directions has rendered these less complete than I had hoped, I shall nevertheless be able to discuss the broad lines of bird evolution upon the basis of their Ischnoceran parasites, and to suggest a certain number of emendations in bird classification.

The Siphunculata are even more specific in their host relations than the Ischnocera, but are not yet well enough known to be of much use in questions of host relationships. Ferris (1919, 1921, 1922, 1923) is engaged in monographing the group, and, when his work is completed, it should be very valuable from this point of view. Kellogg (1913a) has shown that man and the anthropoids share a genus of sucking lice which is distinct from that found upon the lower monkeys.

x.—*The Host-parasite Relation in Other Insects.*

Amongst insects there are many parasitic groups, especially in the Diptera and Hymenoptera. These have not been studied from the point of view of host relations, but my colleague, Mr. A. J. Nicholson, informs me that there does not appear to be any strict specificity towards insect hosts. Phytophagous insects, on the other hand, exhibit in many cases an absolute specificity towards the plants which they parasitize, but so far little attention has been paid to this relation. Dr. G. A. Waterhouse has kindly given me some brief notes upon the food-plants of Australian butterflies. In the genus *Papilio*, species of the subgenus *Pharmacophagus* feed upon *Aristolochia*, rarely upon allied plants; those of the subgenus *Papilio* chiefly upon Rutaceae (more especially citrus fruit trees), but also upon Umbelliferae; those of the subgenus *Cosmodesmus* upon Anonaceae. *Delias* feeds on *Loranthus*, *Elodina* and *Huphina* on *Capparis*, *Catopsilia* and *Terias* on *Cassia*, the Danaida on Asclepiadeae. Many Lycaenids feed upon Leguminosae, others upon *Loranthus*. Satyrids and some Hesperiids feed on monocotyledons, in many cases being limited to single genera, e.g. *Tisiphone* and *Hesperilla* on *Gahnia* and *Trapezites* on *Xerotes*. It is possible that some significance may attach to the fact that these archaic groups are confined to monocotyledonous plants. In any event the whole question of host-parasite relations in insects seems worthy of further study.

xi.—*Conclusion.*

The foregoing far from exhaustive discussion brings out clearly enough, I think, that there is a general specificity underlying obligate host-parasite relations, however much this may, in some groups, be obscured by the interposition of other factors. Parasites have evolved *pari passu* with their hosts and the history of parasitism goes far back in time. Parasites may therefore quite justifiably be used to aid in the solution of problems affecting their hosts in the various ways indicated in my opening remarks. Where evidence can be derived from more than one group of parasites, as for example in the cases of struthious birds and fresh-water crayfishes which I have mentioned, its value is greatly increased.

In conclusion, I should like to plead not only for a wider application of this host-parasite relation to zoological problems in general, but, also, and more particularly, for the more careful collection of all groups of parasites. Any mammal or any bird harbours parasites without and within which may prove of more value in determining its affinities and status than the skin which is usually the sole trophy of the collector. No parasitic group is at all well known, and until this state of affairs is altered the host-parasite method cannot attain to its full usefulness.

References.

ANDREWS, J. M., 1927.—Host-parasite specificity in the Coccidia of Mammals. *Journ. Parasitology*, xiii, pp. 183-194.

CORDERO, E. H., 1927.—Un nuevo Arquianélido, *Stratiodrilus platensis*, n. sp., que habita sobre *Aeglea laevis* (Latr.). *Physis*, viii, 574-577.

CRAM, E. B., 1927.—Bird parasites of the Nematode Suborders Strongylata, Ascaridata and Spirurata. Bull. 140, U.S. Nat. Museum, 465 pp.

DARLING, S. T., 1921.—The distribution of hookworms in the zoological regions. *Science*, N.S., liii, No. 1371, pp. 323-4.

DUNN, E. R., 1925.—The host-parasite method and the distribution of Frogs. *Amer. Naturalist*, lix, pp. 370-375.

FERRIS, G. F., 1919-1923.—Contributions toward a monograph of the Sucking Lice, Stanford University Publications, Pt. i, 1919; Pt. ii, 1921; Pt. iii, 1922; Pt. iv, 1923.

————, 1922.—The Mallophagan Family Trimenoponidae. *Parasitology*, xiv, No. 1, pp. 75-86.

GROEBBELAAR. C. S., 1922.—Some Trematodes in South African Anura and the relationships and distribution of their hosts. *Trans. Roy. Soc. S. Af.*, x, pp. 191-199.

HARRISON, L., 1911.—The taxonomic value of certain parasites. Abstract in *Ann. Rept. Syd. Uni. Sci. Soc.*, 1911-2.

————, 1914.—The Mallophaga as a possible clue to bird phylogeny. *Aust. Zoologist*, i, 1, pp. 7-11.

————, 1915.—Mallophaga from Apteryx, and their significance. *Parasitology*, viii, No. 1, pp. 88-100.

————, 1915a.—The relation of the phylogeny of the parasite to that of the host. *Rept. Brit. Ass. Adv. Sci.*, 1915, pp. 476-7 (Abstract).

————, 1916.—Bird-parasites and Bird-phylogeny. *Ibis*, April, 1916, pp. 254-263. Abstract and discussion in Bull. ccxii, *Brit. Orn. Club*.

————, 1916a.—A preliminary account of the mouth-parts of the Body-louse. *Proc. Camb. Phil. Soc.*, xviii, pp. 207-226.

————, 1919.—Note on the mouth-parts of Lice. *Aust. Zoologist*, i, 7, pp. 214-216.

————, 1922.—On the Mallophagan Family Trimenoponidae. *Aust. Zoologist*, ii, 4, pp. 154-158.

————, 1924.—The migration route of the Australian Marsupial Fauna. *Aust. Zoologist*, iii, 7, pp. 247-263.

————, 1926.—Crucial evidence for Antarctic radiation. *Amer. Naturalist*, lx, pp. 374-383.

————, 1928.—On the genus Stratiodrilus, etc. *Rec. Aust. Mus.*, xvi, pp. 116-121.

————, 1928a.—The composition and origins of the Australian Fauna, with special reference to the Wegener hypothesis. *Rept. Aust. Ass. Adv. Sci.*, Perth, 1926 (in press).

JOHNSTON. S. J., 1912.—On some Trematode parasites of Australian frogs. PROC. LINN. SOC. N.S.W., xxxvii, pp. 285-362.

————, 1913.—Trematode parasites and the relationships and distribution of their hosts. *Rept. Aust. Ass. Adv. Sci.*, Melbourne, 1913, pp. 272-278.

————, 1914.—Australian Trematodes and Cestodes; a study in Zoogeography. *Med. Journ. Aust.*, Sept. 12. Abstract in *Proc. Brit. Assn. Adv. Sci.*, Australia, 1914.

————, 1916.—On the Trematodes of Australian birds. *Proc. Roy. Soc. N.S.W.*, l, pp. 187-261.

KELLOGG, V. L., 1896.—New Mallophaga, i. *Proc. Calif. Acad. Sci.*, vi, pp. 31-168.

————, 1913.—Distribution and species-forming of Ectoparasites. *Amer. Naturalist*, xlvii, pp. 129-158.

————, 1913a.—Ectoparasites of the monkeys, apes and man. *Science*, N.S. xxxviii, pp. 601-2.

————, 1914.—Ectoparasites of mammals. *Amer. Naturalist*, xlviii, pp. 257-279.

KELLOGG and KUWANA, 1902.—Mallophaga from birds. *Proc. Wash. Acad. Sci.*, iv, pp. 457-491.

MEGGITT, F. J., 1924.—The Cestodes of Mammals. London, 282 pp.

MERRILL, E D., 1926.—The influence of the Australian Flora upon the Flora of the Philippines. *Proc. Pan-Pacific Sci. Cong.*, 1923, Vol. i, pp. 323-4.

METCALF, M. M., 1921.—Upon an important method of studying problems of relationship and of geographical distribution. *Proc. Nat. Acad. Sci.*, vi.

————, 1923.—The Opalinid Ciliate Infusorians. Bull. 120, U.S. Nat. Mus., 484 pp.

METCALF, M. M., 1923a.—The origin and distribution of the Anura. *Amer. Naturalist,* lvii, pp. 385-411.

NOBLE, G. K., 1922.—The phylogeny of the Salientia. *Bull. Amer. Mus. Nat. Hist.,* xlvi, pp. 1-87.

——————, 1925.—The evolution and dispersal of Frogs. *Amer. Naturalist,* lix, pp. 265-271.

NYBELIN, O., 1917.—Australische Cestoden. *Kungl. Svenska Vetenskapsakad., Handlingar,* lii, No. 14, 48 pp.

PAINE, J. H., 1912.—The Mallophagan Genus *Heterodoxus. Ent. News,* xxiii, pp. 359-362.

SANDGROUND, J. H., 1926.—Specificity in the Nematode genus Strongyloides. *Journ. Parasitol.,* xii, 2, pp. 59-80.

SNODGRASS, R., 1896.—In Kellogg, New Mallophaga, i, *q.v.*

STILES and HASSALL, 1908.—Index-catalogue of Medical and Veterinary Zoology. Trematoda. Washington.

——————, 1920.—Ditto, Roundworms. Washington.

WARD, H. B., 1926.—The needs and opportunities in parasitology. *Science,* N.S., lxiv, pp. 231-236.

WENYON, C. M., 1926.—Protozoology, 2 vols., London. Baillière, Tindall and Cox.

ZSCHOKKE, F., 1898.—Die Cestoden der Marsupialia und Monotremata. *Denkschr. med-naturw. Gesellschaft,* Jena, Bd. viii.

——————, 1899.—Neue Studien an Cestoden aplacentaler Säugethiere. *Zeitschr. f. wiss. Zool.,* Bd. lxv.

——————, 1907.—*Moniezia diaphana* n. sp. Ein weiterer Beitrag zur Kenntnis der Cestoden aplacentaler Säugethiere. *Centralbl. f. Bakt.,* xliv, Abt. 1.

On the motion of the Chairman, the following resolution was carried in silence, the Members standing: The Members of the Linnean Society record their deep sorrow at the loss of their President, Professor L. Harrison, whose sudden and unexpected death has stricken his colleagues and friends with grief. Australian Science has lost one of its most brilliant zoologists and one of its most inspiring teachers of zoology, and this Society has lost one of its most valuable members whose place will be difficult to fill. The Members express their sympathy with Mrs. Harrison in her sad bereavement.

Dr. G. A. Waterhouse, Hon. Treasurer, presented the balance sheets for the year ending 31st December, 1927, duly certified as correct by the Auditor, Mr. F. H. Rayment, F.C.P.A., Incorporated Accountant; and he moved that they be received and adopted, which was carried unanimously.

No nominations of other Candidates having been received the Chairman declared the following elections for the ensuing Session to be duly made:—

Members of Council: W. R. Browne, D.Sc., R. H. Cambage, C.B.E., F.L.S., W. W. Froggatt, F.L.S., A. J. Nicholson, M.Sc., F.E.S., G. A. Waterhouse, D.Sc., B.E., F.E.S.

Auditor: F H. Rayment, F.C.P.A.